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AESTIVATION IN A PERMIAN LUNGFISH

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It is generally recognized that the survival to modern times of the three living genera of dipnoan fishes — *Epiceratodus* (*Neoceratodus*) of Australia, *Protopterus* of Africa and *Lepidosiren* of South America is due in great measure to adaptations which tide them over the seasonal droughts characteristic of the tropical regions which they inhabit. A primary adaptation lies in their possession of functional lungs which enable them to utilize atmospheric oxygen, supplementing the reduced oxygen content in stagnant waters during drought; indeed, in *Protopterus*, the lung-breathing function has attained such dominance that the fish is unable to survive if air-breathing is not possible.

But air-breathing in itself is not entirely satisfactory as a means of drought survival — particularly if, as may often happen, the stream or pond dries up entirely. The Australian lungfish, under such circumstances, may wallow into the mud, and have some chance of escaping desiccation or enemies. In the African and South American forms, an additional adaptation is present — the development of a technique of aestivation. Members of these genera are rather elongate and eel-like in shape, in contrast to *Epiceratodus* and to primitive lungfishes. On the approach of the dry season the fish burrows in coiled form into the mud, which hardens about it to form a cocoon; an opening from the surface allows the entrance of air, but the amount needed is small, due to a great reduction of metabolic processes. The fish passes into a "summer sleep" comparable in great measure to the hibernation of various northern animals — a phase which ends with the return of the water and the resumption of normal aquatic life.

Nothing has been known until now of the origin of lungfish aestivation. The early lungfishes, as far as known, all had a fusiform body shape fairly comparable to that of the modern *Epiceratodus*, and hence were incapable of coiling in a burrow in the fashion of the elongate-bodied *Lepidosiren* or *Protopterus;* but it is possible that burrowing of some sort accompanied by physiological features of aestivation, might have preceded change in body shape. The lungfish *Gnathorhiza*, characteristic of the Clear Fork Permian of Texas, has been suspected by both the present writers to be related to the *Lepidosiren-Protopterus* group (Romer and Smith 1934, Olson 1951) but there is no strong proof of relationship, and the body structure was unknown.

Some years ago Dr. H. J. Sawin and Mr. Adolph Witte, while engaged in work for the Texas Bureau of Economic Geology were told by a resident of Willbarger County, of a geologic occurrence which local geologists had been unable to interpret. They visited the locality, made collections of the material for the Bureau and informed others, including the present writers, of the incident. In 1952 Mr. Witte took a Harvard field party, including the senior author, to the site; observations and collections were made at that time and on a return visit the following spring.

The locality lies in southern Willbarger County, Texas, on the Reed Ranch, in Section 34, Block 3, H. & T. C. RR., Co. Survey. The area has not been mapped in detail geologically but the horizon appears to be a short distance above the Lueders limestones and hence in the lower part of the Arroyo Formation of the Clear Fork Group, Lower Permian. Gently sloping exposures here run for a hundred yards or so close to the south bank of Minnie's Creek. Between two thin impure limestones lies a bed of red shale. Scattered over the surface are numerous circular discs, somewhat like large checkers, with diameters which are for the most part between 5.5 and 10 cm. The material of the discs is essentially the same as that of the shale bed from which they are derived, but is slightly harder and somewhat more calcareous, so that they tend to weather out of their enclosing matrix. On excavation, these discs are seen to be segments cleaved from vertical cylinders which are thickly spread through the shale, often only a few inches apart. In no case was a complete cylinder seen; the greatest length preserved in a specimen excavated and collected was 28 cm. The cylinders, in general, weather out from the softer shales with a smooth surface; in some instances portions of the surface show slickensides. No upper terminal portions were found; apparently, at the top,

the material of the cylinder blends laterally with the superposed calcareous shale. The lower ends of the cylinders are generally smoothly rounded; in some cases, however, a lower terminal portion has a diameter rather less than the major portion of the "bore".

The great majority of the "checkers" fractured off from the cylinders show no organic material on their surfaces. A fair number, however, show fish remains. In some instances these appear to be scales and other disarticulated elements of small palaeoniscoids Most of the remains, however, are clearly dipnoan in nature. The hardness of the shale and the relatively soft nature of the bone makes preparation difficult, and reliance has been had mainly on the structures seen in section on the disc surfaces or, in some cases, weathering of the external surface of the cylinders. Bony scales and plates are frequently seen in section and in a few specimens fracture has shown scales in surface view, the largest about 20 mm. in greatest diameter. Numerous discs show hollow ribs, neural or haemal arches and fin supports, sometimes in articulated series. Preparation of the basal segment of one of the cylinders (figured) has revealed a considerable portion of a caudal fin of the sort typical of Paleozoic dipnoans. Vertebral arches and fin elements are present, partly as bone, partly preserved as impressions. The vertebral axis, presumably cartilaginous in life, is represented by a vertically oriented band devoid of impressions. The end of the tail, poorly preserved, was curved around the bottom of the cylinder.

While much of the lungfish material suggests a considerable degree of decay and maceration, it seems certain that in many instances we are dealing with cross-sections of complete, or nearly complete lungfish bodies. In a few instances where "articulating" discs composing the greater part of a cylinder have been collected, it is obvious that we are dealing with successive sections of a single fish, larger, frequently rounded, body sections in the upper and middle parts of the series and caudal sections, typically lens shaped, at the lower end. In many cases the internal skeletal materials are rather irregularly scattered across the surface of the section; in others the arrangement of the ribs and fin supports is essentially regular, and toward the disc margins there can be made out body outlines, marked by scale sections with a surrounding layer of darker matrix.

The only lungfishes known from the Clear Fork belong to the genus *Gnathorhiza*, mentioned above; *Sagenodus*, the common Pennsylvanian genus, possibly antecedent to *Ceratodus* and *Epiceratodus*, is not

recorded in Texas above the Wichita group. But while it is probable that the Reed Ranch lungfish is *Gnathorhiza*, no tooth plates have been found there to make identification certain. A second find, however, has produced a number of fragmentary teeth. These are unmistakably the blade-like, shearing teeth of *Gnathorhiza* and are referable to the species *G. dikeloda* rather than *G. serrata*. This locality was discovered by the junior author and Dr. Nicholas Hotton III in 1949 and has been revisited several times since then. The bed in which the cylinders occur is located in north central Knox County, Texas, on the Waggoner ranch. It crops out along a small tributary to Little Mustang Creek in locality K1 of the junior author (see Olson, 1951 p. 104). The age is middle Vale of the Clear Fork Group, Lower Permian. The site is approximately 700 to 800 feet higher in the Clear Fork section than the Reed Ranch locality.

The physical features of the cylinders from the two sites differ in no important particulars. Those from the Vale locality occur in a deep red shale which varies in thickness from two to three feet. Above and below this bed are lighter colored shales that appear to have been deposited under somewhat different conditions. The shale is best exposed along a small arroyo, but crops out sporadically over an area of about an acre. The cylinders are distributed in rather irregular groups of ten to twenty in unevenly spaced areas not much more than a yard square. The longest cylinder encountered measured 45 cm., but as in the case of the Arroyo specimens no upper termination has been identified. The vertical orientation shown in the specimen figured is constant throughout the deposit.

Organic remains in the cylinders from the two localities differ somewhat. The most common remains in the Vale cylinders are ribs, skull plates and scales of *Gnathorhiza* but, although the ribs in some instances suggest the general body shape of the fish, no case in which the scales show the body outline has been observed. As at the Reed Ranch locality, remains of lungfish are found only in a fraction of the cylinders. Scales of small palaeoniscids and infrequent scraps of skulls of some small captorhinid reptile occur in others. More abundant, however, are partial vertebral columns and single vertebrae of the small, worm-like amphibian, *Lysorophus*. In no case have these columns been found in the coiled condition characteristic of *Lysorophus* specimens throughout the Arroyo formation.

There can hardly be any question that the lungfishes from the two localities belong to the same genus. Some question does exist, how-

ever, with respect to specific identity. Two species, *G. serrata* and *G. dikeloda*, are known from the Vale formation, but only the first has been found in the Arroyo (Olson, 1951). Tooth plates of *G. serrata* are small, lower plates ranging from 10 to 12 mm. in length, whereas those of *G. dikeloda* are between 25 and 32 mm. long. The skulls of adult individuals of *G. dikeloda* appear to have been between 75 and 100 mm. long; this would suggest that the skulls of *G. serrata*, unknown as yet, would have a range of between 25 and 35 mm. The fact that the Arroyo and Vale cylinders are comparable in size indicates that they were made by fish of about the same dimensions. There is, however, the puzzling fact that no teeth of the larger species have been found in the Arroyo in spite of very extensive exploration of its exposures. Except at the Reed Ranch locality lungfish remains are exceedingly rare in the Arroyo; only four or five occurrences have been reported, and these have consisted of single teeth. It may well be that *G. dikeloda* was in existence during the Arroyo times, but that it found suitable habitat in few localities in the areas which are now exposed. With increasing aridity during the Vale, the number of habitats and the chance of discovery probably were greatly increased.

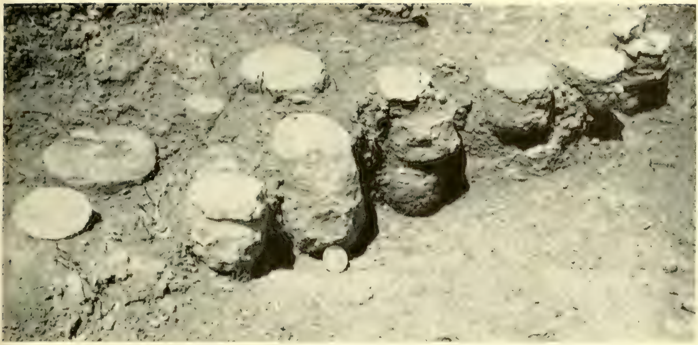
From the data given above, the nature of the phenomena described will be as obvious to the reader as to the authors. We are here surely dealing with evidence of aestivation of lungfish at an early, Paleozoic stage in the history of the Dipnoi. The cylinders are aestivating burrows, made by lungfishes in the muddy bottoms of drying lakes or streams. That most of the cylinders are empty is to be expected; most of the fishes which occupied them survived to the return of the waters and swam away. The burrows were later filled by sediments fairly similar to those which had already formed the mud banks into which they had burrowed. Fortunately, however, the filling material at the localities described was of a somewhat harder, more calcareous, nature than that of the original mud; had they been just the same, differential weathering would not have occurred and the burrows would probably have escaped observation. The lack of definite upper "openings" of the burrows is presumably due to the disturbance of surface materials on the return of the water. The presence of lungfish remains in some of the cylinders indicates that a certain percentage of the aestivating population failed to survive until the return of the waters. The finding of occasional actinopterygian remains in the burrows is due to the presence of palaeoniscid minnows in the returning waters before the burrows had been filled by sediments. This probably applies to the

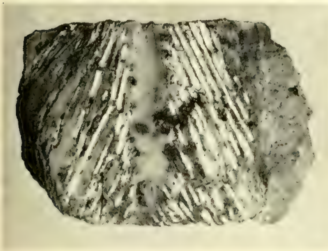
remains of *Lysorophus* as well. This amphibian, like *Gnathorhiza*, had both aestivating and free swimming phases. It characteristically was coiled during aestivation. The fact that coiling has not been observed in the burrows indicates that *Lysorophus* entered the open holes left by the lungfish upon the return of the water, and died during the non-aestivating phase of their existence.

The finding of *Gnathorhiza* teeth in the material from the Vale (KI) locality, together with the absence of identifiable remains of any other lungfish type in the Clear Fork beds makes it seemingly certain that the burrows were made by that lungfish and that alone. This evidence of the adoption of aestivating habits by *Gnathorhiza* strengthens the suggestion, gained from tooth plates and skull pattern, that this genus is possibly ancestral to the modern aestivators, *Lepidosiren* and *Protopterus*. One major difference in the mode of aestivation between modern forms and *Gnathorhiza* may, however, be noted. The Recent genera are elongate, eel-like animals which coil their bodies in a flask-shaped burrow. There has been no previous evidence of body shape in *Gnathorhiza*. The Permiam burrows may be somewhat narrower in their upper portions; they are, however, essentially cylinders rather than "flasks", and in no case is there evidence of more than one section through a fish body at a given level of a burrow. It thus seems certain that the *Gnathorhiza* body was of a normal, non-elongate fusiform shape; that the burrow was formed by a spiral rotation of the body and tail with the fish's long axis in a vertical position; and that the aestivating fish was posed erect in the burrow, essentially "standing on its tail" with the mouth at the top, close to the surface where air was available.

EXPLANATION OF PLATE

Above, a series of exposed burrows at the Reed Ranch locality; a half-dollar gives an indication of size. *Center*, a terminal section of a burrow developed to show an included lungfish tail, its tip curved upward. The skeleton is partly preserved in bone, partly as impressions which have been painted white. At the left, a lateral view of the specimen; at the right, a view from the underside. *Below, left*, a burrow in place at the KI locality; length 45 cm. *Below, right*, an incomplete burrow from the Reed Ranch locality; length 25 cm.





The genus *Gnathorhiza* is known not only from the Texas beds, but also from the late Pennsylvanian of Illinois. In Texas, however, it is very rare in the Wichita formations of the Permian where *Sagenodus*, common in the Pennsylvanian, is fairly abundant: on the other hand, there is no trace of *Sagenodus* in the Clear Fork, where *Gnathorhiza* replaces it. This local succession is in agreement with our beliefs as to the climate of early Texas. Various lines of evidence suggest that Clear Fork time, particularly that of deposition of the Vale and Choza of that group, was one of increasing aridity with marked seasonal variations in rainfall (*cf.* for example Olson, 1948). Accompanying this change is a shift in the local dipnoan fauna from *Sagenodus*, a presumed non-aestivating form, to *Gnathorhiza*, better adapted for survival under drought conditions.

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